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**14. ABSTRACT**
We created a digital system for measurements of extremely low electrical currents in plants. We analyzed and evaluated equivalent electrical circuits in clusters of plant cells and in whole plants and studied the concerted movements and morphing structures induced by electrostimulation of plants and the dynamics of cellular processes. For measurements of force and pressure generated by plants in morphing processes we developed 3 new efficient methods and measured the average impact force of closing the Venus flytrap, morphing force of the trap constriction, and escaping force from the closed trap. We estimated electrical charge, current, resistance, electrical

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## Report Title

Morphing Structures, Mechanosensors, and Osmotic Motors in Plants.

## ABSTRACT

We created a digital system for measurements of extremely low electrical currents in plants. We analyzed and evaluated equivalent electrical circuits in clusters of plant cells and in whole plants and studied the concerted movements and morphing structures induced by electrostimulation of plants and the dynamics of cellular processes. For measurements of force and pressure generated by plants in morphing processes we developed 3 new efficient methods and measured the average impact force of closing the Venus flytrap, morphing force of the trap constriction, and escaping force from the closed trap. We estimated electrical charge, current, resistance, electrical energy and electrical power variation with time during electrostimulation of the morphing trap. We estimated the speed and acceleration of lobe rims during the trap closing. Our results demonstrate that a voltage gated K+ channel in the excitable tissue of plants has properties of a memristor. This study can be a starting point for understanding mechanisms of morphing, memory, learning, circadian rhythms, and biological clocks. This work provides quantitative data on morphing processes, leads to a better understanding of the mechanisms involved in mechanosensing, high speed movements, electrically controlled morphing, and it creates the foundation for the development of advanced sensors, highly efficient noise free motors and morphing structures for future DoD and Air Forces applications.

**Enter List of papers submitted or published that acknowledge ARO support from the start of the project to the date of this printing. List the papers, including journal references, in the following categories:**

**(a) Papers published in peer-reviewed journals (N/A for none)**

| Received | Paper |
|---|---|
| 03/22/2013 15.00 | Alexander G. Volkov, Shawn L. Harris, Chrystelle L. Vilfranc, Veronica A. Murphy, Joseph D. Wooten, Henoc Paulicin, Maia I. Volkova, Vladislav S. Markin. Venus flytrap biomechanics: Forces in the Dionaea muscipula trap, Journal of Plant Physiology, (01 2013): 25. doi: 10.1016/j.jplph.2012.08.009 |
| 03/22/2013 17.00 | J. D. Wooten, V. S. Markin, A. G. Volkov, A. J. Waite. Time Sensors: Circadian Rhythms in Biologically Closed Electrochemical Circuits of Plants, ECS Transactions, (03 2013): 23. doi: 10.1149/05012.0023ecst |
| 03/22/2013 16.00 | Alexander G. Volkov, Chrystelle L. Vilfranc, Veronica A. Murphy, Colee M. Mitchell, Maia I. Volkova, Lawrence O'Neal, Vladislav S. Markin. Electrotonic and action potentials in the Venus flytrap, Journal of Plant Physiology, (02 2013): 0. doi: 10.1016/j.jplph.2013.01.009 |
| 07/19/2014 22.00 | Alexander G Volkov, Victoria Forde-Tuckett, Maya I Volkova, Vladislav S Markin. Morphing structures of the Dionaea muscipula Ellis during the trap opening and closing, Plant Signaling & Behavior, (01 2014): 1. doi: 10.4161/psb.27793 |
| 07/19/2014 21.00 | Alexander G Volkov, Clayton Tucket, Jada Reedus, Maya I Volkova, Vladislav S Markin, Leon Chua. Memristors in plants, Plant Signaling & Behavior, (01 2014): 1. doi: 10.4161/psb.28152 |
| 07/19/2014 20.00 | A. G. Volkov, C. R. Brown. Citrus Greening (Huanglongbing): Fast Electrochemical Detection and Phytomonitoring of the Trees Diseases, ECS Transactions, (04 2014): 9. doi: 10.1149/05823.0009ecst |
| 07/19/2014 24.00 | Alexander G Volkov, Victoria Forde-Tuckett, Jada Reedus, Colee M Mitchell, Maya I Volkova, Vladislav S Markin, Leon Chua. Memristors in the Venus flytrap, Plant Signaling & Behavior, (01 2014): 1. doi: 10.4161/psb.29204 |
| 07/19/2014 23.00 | Alexander Volkov, Jada Reedus, Colee M Mitchell, Clayton Tucket, Victoria Forde-Tuckett, Maya I Volkova, Vladislav S Markin, Leon Chua. Memristors in the electrical network of Aloe vera L., Plant Signaling & Behavior, (01 2014): 1. doi: 10.4161/psb.29056 |
| 07/24/2014 28.00 | Alexander Volkov, Veronica Murphy, Jacqueline Clemmons, Michael Curley, Vladislav Markin. Energetics and forces of the Dionaea muscipula trap closing, J Plant physiology, (01 2012): 55. doi: |
| 07/24/2014 33.00 | Lawrence O'Neal, Lora Ebere, Reuel McIntyre, Maia Volkova-Gugeshashvili, Vladislav Markin, Alexander Volkov. Propagation and Collision of Nonlinear Electrical Responses in Aloe Vera L. and Arabidopsis Thaliana, ECS Transactions, (04 2013): 7. doi: |
| 07/24/2014 38.00 | Alexander Volkov, Astian Waite, Joseph Wooten, Vladislav Markin. Circadian rhythms in biologically closed electrical circuits of plants, Plant Signaling & Behavior, (02 2012): 282. doi: |
| 07/29/2012 8.00 | Vladislav Markin, Alexander Volkov. Morphing structures in the Venus flytrap, Plant Electrophysiology, (05 2012): 0. doi: |

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|---|---|---|
| 08/04/2013 | 19.00 | Alexander G. Volkov, Lawrence O'Neal, Maia I. Volkova-Gugeshashvili, Vladislav S. Markin. Electrostimulation of Aloe Vera L., Mimosa Pudica L. and Arabidopsis Thaliana: Propagation and Collision of Electrotonic Potentials, Journal of ElectroChemical Society, (07 2013): 3102. doi: |
| 08/29/2011 | 1.00 | Alexander G. Volkov, Kara Baker, Justin C. Foster, Jacqueline Clemmons, Emil Jovanov, Vladislav S. Markin. Circadian variations in biologically closed electrochemical circuits in Aloe vera and Mimosa pudica, Bioelectrochemistry and Bioenergetics, (04 2011): 390. doi: 10.1016/j.bioelechem.2011.01.004 |
| 08/29/2011 | 2.00 | Joseph D. Wooten, Alexander G. Volkov, Astian J. Waite, Corydon R. Brown, Vladislav S. Markin. Circadian rhythms in electrical circuits of Clivia miniata, Journal of Plant Physiology, (10 2011): 1753. doi: 10.1016/j.jplph.2011.03.012 |
| 08/30/2011 | 4.00 | Akexander Volkov, Veronica Murphy, Lacqueline Clemmons, Michael Curley, Vladislav Markin. Energetics and forces of the Dionaea muscipula trap closing, Journal of Plant Physiology, (12 2011): 0. doi: |
| **TOTAL:** | **16** | |

**Number of Papers published in peer-reviewed journals:**

## (b) Papers published in non-peer-reviewed journals (N/A for none)

| Received | | Paper |
|---|---|---|
| 07/29/2012 | 9.00 | Emil Jovanov, Alexander Volkov. Plant Electrostimulationand Data Acquisition, Plant Electrophysiology, (05 2012): 45. doi: |
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| **TOTAL:** | | |

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## (d) Manuscripts

| Received | | Paper |
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| 04/18/2012 | 6.00 | Alexander Volkov, Astian Waite, Joseph Wooten, Vladislav Markin. Circadian rhytms in biologically closed electrical circuits of plants, Plant Signaling & Behavior (11 2011) |
| 07/24/2014 | 29.00 | Alexander Volkov, Jada Reedus, Colee Mitchell, Clayton Tucket, Maya Volkova, Vladislav Markin, Leon Chua. Memory elements in the electrical network of Mimosa pudica L., Plant Signaling & Behavior (07 2014) |
| 07/24/2014 | 36.00 | Vladislav Markin, Alexander Volkov, Leon Chua. An analytical model of memristors in plants, Plant Signaling & Behavior (07 2014) |
| 07/24/2014 | 27.00 | Alexander Volkov, Astian Waite, Joseph Wooten, Vladislav Markin. Circadian rhythms in biologically closed electrical circuits of plants, Plant Signaling & Behavior (11 2011) |
| 08/12/2011 | 3.00 | Veronica A. Murphy, Jacqueline I. Clemmons, Michael J. Curley, Vladislav S. Markin , Alexander G. Volkov. Energetics and forces of the Dionaea muscipula trap closing, Journal of Plant Physiology (08 2011) |
| **TOTAL:** | | **5** |

**Number of Manuscripts:**

## Books

| Received | | Book |
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| 04/18/2012 | 5.00 | Alexandre Volkov. Plant Electrophysiology. Methods and Cell electrophysiology, Berlin, New York: Springer, (05 2012) |
| 07/29/2012 | 7.00 | Alexander G. Volkov. Plant Electrophysiology Signaliing and Responses, Berlin, Heidelberg: Springer Berlin Heidelberg, (05 2012) |
| **TOTAL:** | **2** | |

| Received | | Book Chapter |
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| 07/19/2014 | 25.00 | A. G. Volkov, V. S. Markin. Active and Passive Electrical Signaling in Plants, Switzerland: Springer, (09 2014) |
| **TOTAL:** | **1** | |

## Patents Submitted

## Patents Awarded

## Awards

## Graduate Students

| NAME | PERCENT_SUPPORTED |
|---|---|
| **FTE Equivalent:** | |
| **Total Number:** | |

## Names of Post Doctorates

| NAME | PERCENT_SUPPORTED |
|---|---|
| **FTE Equivalent:** | |
| **Total Number:** | |

## Names of Faculty Supported

| NAME | PERCENT_SUPPORTED | National Academy Member |
|---|---|---|
| A. G. Volkov | 1.00 | |
| **FTE Equivalent:** | **1.00** | |
| **Total Number:** | **1** | |

## Names of Under Graduate students supported

| NAME | PERCENT_SUPPORTED | Discipline |
|---|---|---|
| J. D. Wooten | 1.00 | Biology |
| V. A. Murphy | 1.00 | Biochemistry |
| J. C.Foster | 1.00 | Chemistry |
| A. J. Waite | 1.00 | Biochemistry |
| L. O'Neal | 1.00 | Engineering |
| V. Forde-Tuckett | 1.00 | Biology |
| C. Tucket | 1.00 | Biochemistry |
| H. Paulicin | 1.00 | Engineering |
| S. L. Harris | 1.00 | Engineering |
| **FTE Equivalent:** | **9.00** | |
| **Total Number:** | **9** | |

## Student Metrics

This section only applies to graduating undergraduates supported by this agreement in this reporting period

The number of undergraduates funded by this agreement who graduated during this period: ..... 8.00

The number of undergraduates funded by this agreement who graduated during this period with a degree in science, mathematics, engineering, or technology fields:..... 8.00

The number of undergraduates funded by your agreement who graduated during this period and will continue to pursue a graduate or Ph.D. degree in science, mathematics, engineering, or technology fields:..... 7.00

Number of graduating undergraduates who achieved a 3.5 GPA to 4.0 (4.0 max scale):..... 6.00

Number of graduating undergraduates funded by a DoD funded Center of Excellence grant for Education, Research and Engineering:..... 0.00

The number of undergraduates funded by your agreement who graduated during this period and intend to work for the Department of Defense ..... 1.00

The number of undergraduates funded by your agreement who graduated during this period and will receive scholarships or fellowships for further studies in science, mathematics, engineering or technology fields:..... 4.00

## Names of Personnel receiving masters degrees

| NAME |
|---|
| **Total Number:** |

## Names of personnel receiving PHDs

| NAME |
|---|
| **Total Number:** |

## Names of other research staff

| NAME | PERCENT_SUPPORTED |
|---|---|
| M. I. Volkova | 1.00 |
| **FTE Equivalent:** | **1.00** |
| **Total Number:** | **1** |

## Sub Contractors (DD882)

## Inventions (DD882)

## Scientific Progress

See Attachment

## Technology Transfer

**Morphing Structures, Mechanosensors, and Osmotic Motors in Plants**
**Final Report**

Many plants have the ability to morph and become a shape-changer with optimal performance with low turning radius, long endurance, and high speed. Our project exploits a new approach to the problem of plant morphing structures. We established new collaborative relationships with Professor V. S. Markin (University of Texas, Dallas) and published articles in peer-review journals, review-chapters and two books on plant electrophysiology and electrically controlled morphing structures in plants. Our specific aims are as follows: 1) Developing the system for low electrical currents measurements in clusters of plant cells and whole plants and evaluation of the threshold electrical charge, which can induce the plant movement; 2) Studying the concerted movements and morphing structures in plants induced by electrostimulation of biologically closed plant electrical circuits and the dynamics of cellular processes under environmental stress; 3) Using the basic hydroelastic model of the Venus flytrap and *Mimosa pudica* for identification and interpretation of plant movement and morphing structures; 4) Developing models of mechanosensory effects and morphing structures in plants (*Mimosa pudica* and the Venus flytrap) and their correlation with electrical plant memory; 5) Broadening the participation of individuals from underrepresented groups in the area of natural materials and systems supported by the AFOSR.

**1. Developing the system for low electrical currents measurements in clusters of plant cells and whole plants and evaluation of the threshold electrical charge, which can induce the plant movement.**

We created a new system for measurements of extremely low electrical currents in plants using a new electronic high speed switch and a new Guard and Current Amplifier Module NI PXI-4022 for low current measurements, which is connected to NI-PXI DMM to decrease electrical noise in the experimental setup. Multichannel high speed USB data acquisition card NI-USB 6255 was interfaced to a computer. We developed a new software package for plant electrophysiology, based on LabView program from National Instruments. We studied electro stimulated by a function generator or our new Charge Stimulating Method the hydromechanical concerted movements in plants and synchronous video recording of plant movements. The charge is delivered from a capacitor that is charged at a selected potential. When capacitor with capacitance C is connected to the source with voltage U, the total capacitor charge is Q = CU, which allows precise regulation of the amount of charge during stimulation by using different capacitors and applying various voltages. Experimentation with electrical stimulation of plants requires precise control of plant electrical parameters. The charged capacitor provides the electrical trigger that unleashes the long chain of events with their own sources of energy. This energy is accumulated in plants most probably in hydraulic form. Therefore, our Charge Stimulating Method estimates the trigger energy, and then we estimate kinetic energy of the moving parts of a plant. We analyzed and evaluated equivalent electrical circuits in clusters of plant cells and in whole plants. We investigated effects of uncouplers, inhibitors of ion channels and aquaporins on kinetics of plant movements and electrical signals transduction in *Mimosa pudica* and the Venus flytrap.

## 2. Studying the concerted movements and morphing structures in plants induced by electrostimulation of biologically closed plant electrical circuits and the dynamics of cellular processes under environmental stress

All biological organisms continuously change their shapes both in the animal kingdom and in plant kingdom. These changes reveal the internal properties of plants. Among them there are fascinating examples that are able to morph extremely fast under electrical control. They not only adjust to the changing environment but they also receive signals from the external world, process those signals and react accordingly. The world "morphing" is defined as efficient, multi-point adaptability and may include macro, micro, structural and/or fluidic approaches.

Some carnivorous plants are able to attack their preys. The most famous of these is the Venus flytrap (*Dionaea muscipula* Ellis). This is a sensitive plant whose leaves have miniature antennae or sensing hairs that are able to receive, process, and transfer information about an insect's stimuli. Touching trigger hairs, protruding from the upper leaf epidermis of the Venus flytrap, activates mechanosensitive ion channels and generates receptor potentials, which can induce action potentials. It was found that two action potentials are required to trigger the trap closing. When trigger hairs in the open trap receive mechanical stimuli, a receptor potential is generated. Receptor potentials generate action potentials, which can propagate in the plasmodesmata of the plant to the midrib. Uncouplers and blockers of fast anion and potassium channels inhibit action potential propagation in the Venus flytrap. The trap accumulates the electrical charge delivered by an action potential. Once a threshold value of the charge is accumulated, ATP hydrolysis and fast proton transport starts, and aquaporin opening is initiated. Fast proton transport induces transport of water and a change in turgor. The Venus flytrap in nature is normally brought into action by mechanical stimulation. However we recently found that the trap of the Venus flytrap can be also closed by electrical stimulation. The electrical stimulus between a midrib and a lobe closes the Venus flytrap upper leaf in 0.3 s without mechanical stimulation of trigger hairs. For the first time, we developed two new methods for force measurements in plants. We measured the closing force of the trap of *Dionaea muscipula* Ellis after mechanical or electrical stimulation of the trap using the piezoelectric thin film or tactile pressure indicating sensor film. We found that the closing force is 0.14 N and the corresponding pressure between rims of two lobes was 41 kPa. We evaluated theoretically, using the Hydroelastic Curvature Model velocity, acceleration and kinetic energy from the time variation of distance between rims of lobes during the trap closing and compared with experimental data. The Charge Stimulation Method was used for trap electrostimulation between the midrib and lobes. From the dependence of voltage between two Ag/AgCl electrodes in the midrib and one of the lobes, we estimated electrical charge, current, resistance, electrical energy and electrical power variation with time during electrostimulation of the trap.

Mechanical reactions in plants are based on mechanosensory effects, electrical signal transduction, and morphing structures. Our novel non-invasive methods give insight into mechanisms of different steps of signal transduction and mechanical responses in the plant kingdom. We exploited a new approach to the problem of plant biomechanics and electrical engineering in vivo. Progress toward characterization of the nature and extent of electrical signal transduction in plants opens new avenues for control of plant biomechanics. We demonstrated mechanisms of concerted movements in plants from electrical signal transduction to cascades of cellular events. We measured forces and pressure inside the Venus flytrap in response to a prey struggling by two different methods and got the coinciding results. This is the first attempt to measure mechanical forces inside plants.

The driving force of the closing process is most likely the elastic curvature energy stored and locked in the leaves due to a pressure difference between the upper and lower layers of the leaf. The open state of the trap contains high elastic energy accumulated due to the hydrostatic pressure difference between the hydraulic layers of the lobe. The trigger signal opens the water pores between these layers and the fluid transfers from the upper to the lower layer. The leaf relaxes to its equilibrium state, corresponding to the closed configuration.

We have estimated the energetics of trap movement and triggering energy of the trap. The kinetic energy of the moving lobe changes in the process of closing and reaches the maximum of 0.49 microJ. It happened to be much smaller than the triggering energy of the charged capacitor equal to 8.4 microJ. A portion of this triggering energy is certainly lost to heat and the rest goes to the initiation of hydraulic and mechanical transformations in the leaf.

***Trap closing average impact force measurement: Piezoelectric sensor***. It is important to measure the average impact force in carnivorous plants. In the process of closing, the lobes of the Venus flytrap move very quickly and rims of the lobes hit each other with a certain force. Our goal is to measure this force. It can be achieved with help of piezoelectric sensor which can measure the force of this strike between rims (Fig. 1). The piezoelectric force measurement is based on the piezoelectric effect. Piezoelectric measuring systems are active electrical systems, which produce an electrical output only when they experience a change in load. They offer excellent quasistatic measuring capability, but they cannot perform true static measurements. A very high input impedance data acquisition board can record their voltage, which is proportional to mechanical loading.

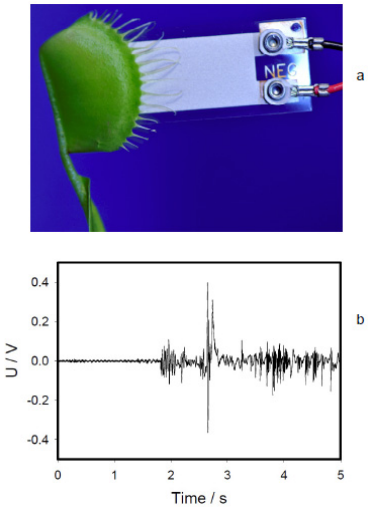


Figure 1. (a) Insertion of the piezoelectric film PZ-03 into trap; (b) Electrical response of the piezoelectric film PZ-03 on the trap closing and locking.

The sensor film was lowered vertically between two lobes above the midrib (Fig. 1). The average impact force of the trap closing was measured by the piezoelectric sensor PZ-03 (Images Scientific Instruments). Piezoelectric film has a thin urethane coating over the active sensor area. The size of film was 6 mm x 41 mm x 0.2 mm. For the calibration of the dependence of the sensor electrical response on the applied force, laboratory standard weights (Fisher Scientific), were dropped on the piezoelectric sensor film from 7 cm above PZ-03. Digital high speed video camera was used to measure the height of standard weights traveled after impact and duration of contact between the moments of the impact and bounce. For calibration of the piezoelectric sensor electrical response, we dropped different weights on the piezoelectric sensor film from 7 cm above PZ-03. Average impact force was estimated from the following equation for elastic impact.

In this derivation we defined direction up as positive and direction down as negative. Let $h_1$ be the height from which a weight was dropped, $h_2$ is the height of bounce after impact. Then velocities at the beginning $v_1$ and at the end $v_2$ of contact are equal to

$$v_1 = -\sqrt{2gh_1}; \qquad v_2 = \sqrt{2gh_2} \tag{1}$$

According to the Newton's second law, the net force is the rate of change of its linear momentum $\boldsymbol{p} = m\boldsymbol{v}$ in inertial reference frame. For the falling weight of mass $m$, we can write for the elastic impact:

$$m(v_2 - v_1) = (F_{average} - mg)\,\tau \tag{2}$$

or

$$F_{average} = \frac{m(v_2 - v_1)}{\tau} + mg\,, \tag{3}$$

where $g$ is the acceleration due to gravity, $\tau$ is a duration of contact between the moments of the impact and bounce.

Average acceleration is equal to

$$a_{average} = \frac{v_2 - v_1}{\tau} + g = \frac{\sqrt{2gh_1} + \sqrt{2gh_2}}{\tau} + g = \frac{\sqrt{2g}\left(\sqrt{h_1} + \sqrt{h_2}\right)}{\tau} + g \tag{4}$$

and the average impact force for the elastic impact is equal to

$$F_{average} = ma_{average} = \frac{m\sqrt{2g}\left(\sqrt{h_1} + \sqrt{h_2}\right)}{\tau} + mg\,. \tag{5}$$

High speed video recording was used to measure $h_2$ and $\tau$. The electrical signal was measured using a NI PXI-6115 DAQ.

When the Venus flytrap catches the insect it does not crush the prey but rather hugs it by building the cage around it. This is achieved by bending the lobes. The curvature of the lobes changes during closing of the trap from convex to concave configuration. The trap changes from a convex to a concave shape in about 100 ms. There is a very small tightening of lobes during the first five minutes. Cilia on the rims of the lobes bend over and lock the edges. The trap can stay in such a position for a few hours before opening if the prey is too small for digesting.

Upon closure, the cilia protruding from the edge of each lobe form an interlocking wall that is impenetrable to all except the smallest prey. The trap uses the double-trigger mechanism and shuts when the prey touches its trigger hairs twice in succession within a 25-second window of time. Partial closure allows the cilia to overlap, however the lobes are still held slightly ajar. This partial closure occurs in a fraction of a second, and several minutes may be required for the lobes to come together fully. When a prey is caught, the lobes seal tightly and thus remain for 5-7 days, allowing digestion to take place. Since the area of lobes contact during the trap closing was $3.64 \times 10^{-6}$ m$^2$ , we can estimate approximate pressure by dividing force by the area of contact, which is equal to 0.149 N/0.00000364 m$^2$ = 40.9 kPa. We found that the trap closing force is 0.149 N and pressure between rims of the lobes is 40.9 kPa. Due to this reason, when the Venus flytrap catches large enough insects, they can't move outside the trap due to high pressure between the rims. For digesting the prey, the Venus flytrap needs to compress lobes and decrease volume inside the trap and distance between the lobes. This process we call the constriction of the trap. We used gelatin as a prey model. Forces of constriction can rich 0.45 N. Since the cross surface area of a gelatin filled sponge was 0.5 cm$^2$, we can estimate the constriction pressure which is equal to 0.45 N/0.00005 m$^2$ = 9 kPa. Both methods of pressure measurements gave approximately the same value of the constriction pressure. The pressure between the rims of the

lobes is 4.5 times higher than the constriction pressure between lobes. According to equation (7), the initial holding prey force is equal to 0.188 N immediately after the trap is closed. This force is slightly higher than the trap's closing force of 0.149 N. During the gelatin digestion, the escaping force increases to 3.9 N.

Strong tightening of the rims is important for the Venus flytrap to keep a prey inside the trap and to avoid leaking from the trap during the prey digestion.

**3. Using the basic hydroelastic model of the Venus flytrap and *Mimosa pudica* for identification and interpretation of plant movement and morphing structures**

It is important to understand the mechanics of the trap closure. One could compare the leaf of this plant to the open book with a fly sitting on the page; the fly can be caught by swift shutting of the book. However, this comparison would be very wrong. In the "book model" there is a pivot at the midrib of the leaf and two flat parts of the book would rotate around this pivot and crush the poor fly. Actual closing of the trap occurs in a different way. The midrib is not a pivot. In the open state (cocked state) the lobes of the leaf have the convex shape (Fig. 2). Angle α is the initial angle between the lobe and the vertical line at the midrib. The total angle between two lobes at the midrib is 2α. This angle does not change (at least does not change noticeably) in the process of trap closing. The lobes do not rotate around the midrib, but only change their curvature. As a result the distant parts of the leaf move in the space and approach each other – the trap closes. Every point $\xi$ of the lobe moves with different velocity $v(\xi,t)$.

In this analysis we designated the width of the lobe by $L$. The initial radius of curvature is $R$, ξ is an arbitrary point along the leaf with corresponding angle γ. We measured a number of typical leafs of Venus flytraps to find the following averaged parameters: $\alpha = 34^o = 0.593$ rad, length $L = 2$ cm. These two parameters remain constant. The angle at the center of curvature is β. It changes in the process of closing; its initial value is $\beta_1 = 52^o$, initial radius of curvature is $R_1 = 2.2$ cm, or curvature $C_1 = 0.454$ cm$^{-1}$. After closing angle $\beta$ changes to $\beta_2 = -2\alpha = -1.186$ rad, $C_2 = -0.593$ cm$^{-1}$.

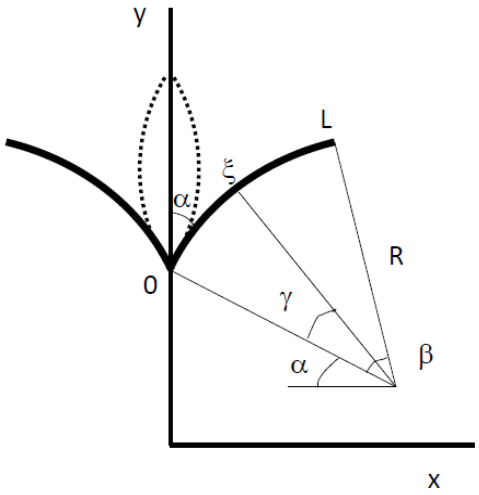


Fig. 2. Description of the model: transition from open (solid lines) to closed state (dashed lines). The system has cylindrical symmetry and the leaf (from 0 to $L$) is modeled as a circle. $L$ – the length of the leaf; β - angle at the center of this circle; $R$ – radius of curvature ; α – initial angle at the midrib (does not change); $\xi$ – an arbitrary point at the leaf; and γ - the angle at the center of curvature corresponding to this point $\xi$.

**4. Developing models of mechanosensory effects and morphing structures in plants (*Mimosa pudica* and the Venus flytrap) and their correlation with electrical plant memory.**

The accumulated data suggest that elastic energy does play an important role, but driving force behind this event involves another process that determines the transformation from an open to a closed state. The *Hydroelastic Curvature Model* includes bending elasticity, turgor pressure,

and water jets. The closure of the Venus flytrap represents the nonmuscular movement based on hydraulics and mechanical elasticity. The nastic movements in various plants involve a large internal pressure (turgor) actively regulated by plants.

In the *Hydroelastic Curvature Model* the leaf of Venus fly trap is visualized as a thin, weakly-curved elastic shell with principal natural curvatures that depend on the hydrostatic state of the two surface layers of cell A and B, where different hydrostatic pressures $P_A$ and $P_B$ are maintained.

Two layers of cells, mechanically connected to each other, behave like a very popular in membrane mechanics bilayer couple where the in-plane expansion or contraction of any of them causes the change of curvature of the whole leaf. The bilayer couple hypothesis was first introduced by Sheetz and Singer (1974). They noticed that the proteins and the phospholipids of membranes are asymmetrically distributed in the two halves of the bilayer, which is most substantial for the erythrocyte membrane. The two halves of the closed membrane bilayer may respond differently to various perturbations while remaining coupled to one another. One half of the bilayer may expand in the plane of the membrane relative to the other half of the bilayer, while the two layers remain in contact with one another. This leads to various functional consequences, including shape changes of the intact cell. This concept is called the bilayer couple hypothesis because of the analogy to the response of a bimetallic couple to changes in temperature. It remains very popular and applied to explanation of numerous phenomena, such as red blood cell transformations and the gating of mechanosensitive channels.

The bilayer couple properties were also extensively studied in connection with bilayer fusion, fission, endo- and exocytosis. This technique was applied for the design and analysis of the hydroelastic curvature model of the Venus flytrap. The model is based on the assumption that the driving force of closing is the elastic curvature energy stored and locked in the leaves due to pressure differential between the outer and inner layers of the leaf.

Unequal expansion of individual layers A and B results in bending of the leaf, and it was described in terms of bending elasticity. Unequal expansion means that the torque $M$ appears in the leaf. The energy of the bent layer A is described by the equation

$$E_A = \frac{1}{2}\kappa_0 \left(C_{AM} - C_{A0}\right)^2 + \kappa_G C_{AG} \qquad (8)$$

Here $C_{AM}$ is the total curvature of the layer A, $C_{AG}$ is the Gaussian curvature, $C_{A0}$ is the spontaneous or intrinsic curvature of the layer, and κ designates the elasticity. Usually spontaneous curvature of layers is considered a constant $b_A$, depending on the composition of the layer, and describes the intrinsic tendency of the layer to bend. There is an additional source of bending – different pressure in two adjacent layers. One can easily visualize the number of mechanical models in which spontaneous curvature is proportional to the pressure in which curvature is $C_{A0} = a_A P_A + b_A$. The same equations are valid for layer B.

The geometrical mean and Gaussian curvatures are defined as $C_{AM} = 1/R_1 + 1/R_2$ and $C_{AG} = 1/\left(R_1 R_2\right)$, where $R_1$ and $R_2$ are the main radii of curvature of the layer. The shape of the leaf was approximated by a spherical surface; then $C_{AM} = 2/R$ and $C_{AG} = {C_{AM}}^2/4$. The leaf is thin and hence the two layers have the mean curvatures that are equal in absolute value but have opposite signs: $C_{AM} = -C_{BM} = C_M$ . The sign of curvature was defined with respect to the normal directed outside of the layer (Fig. 10). Total elastic energy of the lobe was presented as

$$E_L = \frac{1}{2}\kappa_0\left[\left(C_M - a\,P_A - b_A\right)^2 + \left(-C_M - a\,P_B - b_B\right)^2\right] + \frac{1}{2}\kappa_G C_M^2 \qquad (9)$$

Here, the coefficients $a_A$ and $a_B$ are assumed to be equal to $a$.

At the given pressures $P_A$ and $P_B$, the equilibrium value of the mean curvature can be found from the minimum value of elastic energy (9):

$$C_M = \frac{1}{2 + \kappa_0/\kappa_G}\left[a\left(P_A - P_B\right) + b_L\right] \qquad (10)$$

Here $b_L$ designates the difference between two intrinsic curvatures, $b_L = b_A - b_B$. This equilibrium shape is maintained if the pressure difference does not change.

In the open state, the pressure in the upper layer is higher than in the lower layer, maintaining the convex shape of the leaf. The fact, that the hydrostatic pressure in different parts of the plant can vary, is very well known. It is also known (Tamiya et al., 1988) that stimulation of a *Mimosa* plant causes very fast redistribution of water. Tamiya et al (1988) found that after stimulation, water in the lower half of the main pulvinus is transferred to the upper half of the main pulvinus. Movement of the water in conjunction with *Mimosa* movement was visualized by a non-invasive NMR imaging procedure (Detmers 2006). This fast water redistribution is obviously driven by the pressure difference between different parts of the plant, and exchange occurs through open pores. Unfortunately, the anatomy and the nature of these pores are not currently known. So, for the mechanical analysis their existence was simply accepted.

At the resting state water pores between the two hydraulic layers are closed. The external trigger, either mechanical or electrical, results in the opening of these connecting pores; water rushes from the upper to the lower layer, the bilayer couple quickly changes its curvature from convex to concave and the trap closes.

If the trigger reaches threshold value at the moment $t_s$ and the characteristic time of the opening kinetics is $\tau_a$ then the open probability of the pores (after $t \geq t_s$) will be given by $n_{op}(t) = 1 - Exp\left[-\left(t - t_s\right)/\tau_a\right]$. The rate of fluid transfer can be presented as $J = n_{op} L_H \left(P_A - P_B\right)$, where $L_H$ is the hydraulic coefficient of pore permeability. If the pressure in the layer is proportional to the amount of fluid confined in it, the pressure will change with a rate proportional to the fluid transfer between the layers: $dP_A/dt = -k_r J = -dP_B/dt$. This means that the sum of the two pressures remains constant: $P_A + P_B = const = P_{total}$. Then the variation of pressure can be described by the equation

$$\frac{dP_A}{dt} = -k_r n_{op} L\left(P_A - P_B\right) = -\frac{n_{op}}{\tau_r}\left(P_A - \frac{1}{2}P_{total}\right) \qquad (11)$$

Here the characteristic time of fluid transfer, $\tau_r = 1/\left(2k_r L_H\right)$, is introduced. A similar equation for the mean curvature can be easily obtained from eqs. (10) and (11):

$$\frac{dC_M}{dt} = -\frac{n_{op}}{\tau_r}\left(C_M - \frac{b_L}{2 + \kappa_G/\kappa_0}\right) \qquad (12)$$

Initial curvature $C_1$ in the open state can be introduced arbitrarily, while the final curvature $C_2$ in the closed state is found from eq. (12) automatically: $C_2 = \frac{b_L}{2 + \kappa_G/\kappa_0}$.

When solving this equation, one has to have in mind that the open probability $n_{op}$ is the function of time found above. If initial mean curvature at the moment $t = t_s$ is $C_M = C_1$ , the solution of eq. (12) at $t \geq t_s$ is

$$C_M(t) = (C_1 - C_2) \exp\left\{\frac{\tau_a}{\tau_r}\left[1 - \exp\left(-\frac{t - t_s}{\tau_a}\right)\right] - \frac{(t - t_s)}{\tau_r}\right\} + C_2 \qquad (13)$$

When experimentally observing the closing of the Venus flytrap, one can register the change of leaf curvature, but it is easier to measure the change of the distance, $X$, between the edges of the leaves of the Venus flytrap. Let us designate the initial distance as $X_1$, and the final distance as $X_2$. We shall use the normalized distance defined as $x = X/X_1$ . It was shown that both distance and mean curvature of the leaf are described by the same function of time.

When the trigger signal opens the pores between the hydraulic layers at the moment $t = 0$, the fluid rushes from one layer to another. The leaf relaxes to its equilibrium state corresponding to the closed configuration. The distance between the edges of the trap was found to vary with time as

$$x(t) = (1 - x_2) \exp\left\{\frac{\tau_a}{\tau_r}\left[1 - \exp\left(-\frac{t - t_s}{\tau_a}\right)\right] - \frac{(t - t_s)}{\tau_r}\right\} + x_2 \qquad (14)$$

This function was experimentally verified by studying the closure of the Venus flytrap.

The Venus flytrap can be closed by mechanical stimulation of trigger hairs using a cotton thread or wooden stick to gently touch one or two of the six trigger hairs inside the upper leaf of the Venus flytrap. The cotton thread was removed before the leaves closed. It could also be closed by small piece of gelatin. Plants were fed a 6 mm x 6 mm x 2mm cube of 4 % (w/v) gelatin. This induces closing by stimulating 2 of the 6 trigger hairs of the Venus flytrap.

The Venus flytrap could also be closed by an electrical pulse between the midrib and a lobe of the upper leaf without mechanical stimulation. The closing was achieved by electrical stimulation with a positive electrode connected to the midrib and a negative electrode located in one of the lobes. It is interesting that inverted polarity pulse was not able to close the plant, and the closed trap would not open by electrical stimulus lasting up to 100 s.

A single electrical pulse exceeding a threshold (mean 13.63 μC, median 14.00 μC, std. dev. 1.51 μC, n = 41) causes closure of a trap and induces an electrical signal propagating between the lobes and the midrib. When charges were smaller, the trap did not close. Repeated application of small charges demonstrates a summation of stimuli. Two or more injections of electrical charges within a period of less then 50 s closed the trap as soon as a total of 14 μC charge is applied. Traps closing by electrical stimulus obey the all-or-none law: there is no reaction for stimulus under the threshold and the speed of closing does not depend on stimulus strength above threshold.

Theoretical curve and experimental points in Figure 3 show the kinetics of closing the upper leaf induced by mechanical or electrical stimuli. Closing consists of three distinctive phases.

Immediately after stimulation, there is a mechanically silent period with no observable movement of the plant. This is followed by a period when the lobes begin to accelerate. The third period of fast movement is actual trapping when the leaves quickly relax to the new equilibrium state. The processes of closing by mechanical or electrical stimuli qualitatively are very similar though parameters of these processes are somewhat different. These parameters were found from curve fitting. The closing develops at just a fraction of a second. The first mechanically silent

phase lasts 110 ms and the opening of water channels takes between 10 and 20 ms. These two stages are about two times faster with mechanical stimulation than with electrical one. However, this is not the case for relaxation stage: it is two times slower with mechanical stimulation. Therefore, the fastest stage both with mechanical and electrical stimulation is the opening of water channels. The limiting stage of the process is the fluid transfer in the leaf, though it is also very quick due to the small distance between the layers. In both experiment the characteristic time $\tau_a$ is always less than $\tau_r$. This means that pore opening is relatively fast and it is not a limiting stage. Final relaxation of the trap to the closed state is much slower.

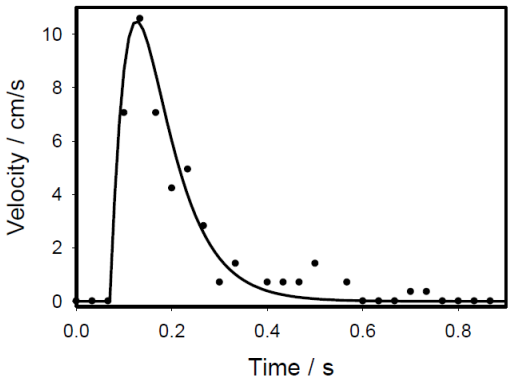


Figure 3. Speed of the trap closing induced by mechanical stimulation of *D. muscipula*. Solid line – theoretical estimation from equation 9. From the curve fitting we found the following parameters: $t_s = 0.07$ s, $\tau_a = 0.05\,s$, $\tau_r = 0.07$ s, $(1-x_2)X_1 = 1.5$ cm/s.

***Memristors in plants: electrical memory and morphing***

The standard electrical circuits comprise four basic elements: a resistor, a capacitor, an inductor, and a memristor. The fourth basic circuit element is a memristor, or a resistor with memory. Memristors are memory circuit elements whose properties depend on the history and state of the system. Here we are going to analyze the memristance in different plants.

A memristor is a nano-scale memory device, which has huge potential technical applications. A memristor is a nonlinear element because its current-voltage characteristic is similar to that of a Lissajous pattern observed from nonlinear systems. No combination of nonlinear resistors, capacitors and inductors can reproduce this Lissajous behavior of the memristor. It is a fundamental 2-terminal electrical circuit element described by a state-dependent Ohm's Law. A voltage-controlled memristor can be defined by

$$I = G(x_1, x_2 ... x_n; V)V$$
$$\frac{dx_k}{dt} = f_k(x_1, x_2 ... x_n; V), k = 1, 2, ...n \quad (15)$$

where $G$ is the memductance of the memristor. The "n" state variables ($x_1, x_2, ..., x_n$) depend on the internal state of the memristor and is defined by "$n$" 1st-order differential equations called the associated state equations. A current-controlled memristor is defined by

$$V = M(x_1, x_2 ... x_n; I)I$$
$$\frac{dx_k}{dt} = f_k(x_1, x_2 ... x_n; I), k = 1, 2, ...n \quad (16)$$

where $M$ is the memristance of the memristor. The unit of the memristance is the Ohm. The unit of the memductance is the Siemens. Mathematically memristance can be described by equation:

$$M(q(t)) = \frac{d\varphi(q)}{dq} = \frac{\left(\frac{d\varphi}{dt}\right)}{\frac{dq}{dt}} = \frac{V(t)}{I(t)} \quad (17)$$

where $\varphi$ and $q$ denote the flux and charge, respectively.

Chua found that a memristor has three characteristic fingerprints: "When driven by a bipolar periodic signal (such as sine waves with zero average value) the device must exhibit a pinched hysteresis loop in the voltage-current plane, assuming the response is periodic; starting from some critical frequency, the hysteresis lobe area should decrease monotonically as the excitation frequency increases; the pinched hysteresis loop should shrink to a single-valued function when the frequency tends to infinity". However, in a plant tissue, the pinched hysteresis loop transforms to a non-pinched hysteresis loop instead of a single line $I = V/R$ at high frequencies of the applied voltage because the amplitude of electrical current depends also on the capacitance of the plant tissue and electrodes, the scanning frequency and direction of scanning:

$$I = C\frac{dV}{dt} \qquad (18)$$

where the capacitance $C$ had been observed to be also a function of scanning frequency.
The pinched hysteresis loop of memory elements, when subject to a periodic stimulus, can be self crossing (type I memristor) or not (type II memristor). We are first who found memristors in different plants.

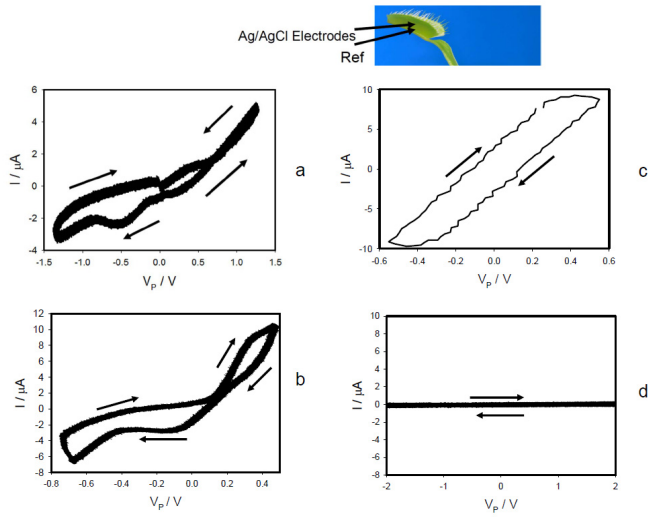


Figure 4. Dependencies of electrical current, $I$, in the Venus flytrap on $V_P$ induced by triangle voltage wave $V_{FG}$ from a function generator (a,b,c,d); Frequency of triangle voltage $V_{FG}$ scanning was 0.001 Hz (a,b,d) and 10 Hz (c); Effects of voltage gated channel inhibitor TEACl (d) deposited on the midrib of the Venus flytrap 5 hours before electrical measurements. R = 47 kOhm. Position of Ag/AgCl electrodes in the Venus flytrap is shown. The trap was open in (b,c,d) or closed in (a).

Figure 4 shows the results of electrostimulation of the Venus flytrap by a bipolar triangle wave with amplitude of ±1V and frequency of 0.001 Hz for closed trap (panel a) and for an open trap (panel b). In both cases we obtained a pinched hysteresis loop in the voltage-current plane with one important difference. Pinched hysteresis loop is a double-valued Lissajous figure of (V(t), i(t)) for all times t, except when it passes through the origin, where the loop is pinched If the trap is closed, the plot displays a common pinched point with self-crossing between curves when $I$ = 0 μA and $V_P$ = 0 V (Fig. 4a). If the trap is open, the plot also displays a common pinched point but without self-crossing between curves with coordinates $I$ = 1.5 μA and $V_P$ = 0.16 V (Fig. 4b). This deviation of coordinates $V_P$ and $I$ from zero value can be caused by the action potential propagation in the trap, which has amplitude of 0.16 V. Increasing of a triangle wave frequency to 1 kHz changes the shape of the line: it is still a loop but without pinched point if the trap is open (Fig. 4c) as well as if the trap is closed. The branches go parallel to each other. So, the electrostimulation of the Venus flytrap by a periodic wave induces electrical responses in the Venus flytrap with fingerprints of a memristor. Voltage gated ionic channels regulate

generation and transduction of electrical signals. For their analysis there are very efficient tools - blockers of ionic channels. It was intriguing to investigate if these blockers would change characteristics or even the presence of memristors in plants. Tetraethylammonium chloride (TEACl) is known as a blocker of a voltage gated $K^+$ channel. We found that deposition of 20 μL of 10 mM TEACl on the midrib decreased the amplitude of electrical current and the hysteresis shrank. Figure 4d shows that five hours after the TEACl deposition to the midrib, the pinched point in the hysteresis loop in the voltage-current plane disappears. The $I$-$V_P$ hysteresis loop appears as a single line because the amplitude of electrical current, $I$, decreases 25 times. This can be caused by the increasing of resistance between electrodes in the plant tissue. Tetraethylammonium chloride transforms a memristor to a resistor in plant tissue. These results demonstrate that a voltage gated $K^+$ channel in the excitable tissue of the Venus flytrap is a plant memristor.

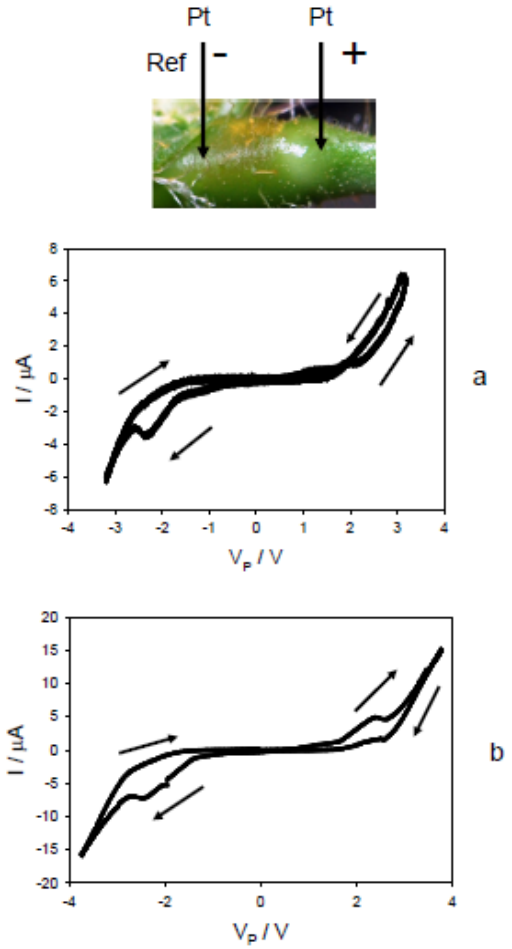


Figure 5. Dependencies of electrical current, $I$, on voltage $V_P$ applied along a pulvinus. Frequency of sinusoidal voltage scanning was 0.001 Hz. R = 47 kOhm. Position of Pt electrodes in the pulvinus of the *Mimosa pudica* is shown. Amplitude of applied voltage $V_{FG}$ from a function generator varies from -3.5 V to + 3.5 V (a) and from -4.5 V to + 4.5 V.

The *Mimosa pudica* is a nyctinastic plant that closes its leaves in the evening. The leaves open in the morning due to a circadian rhythm, which is regulated by a biological clock with a cycle of about 24 hours. Leaf movement in the *Mimosa pudica* appear to be regulated by electrical signal transduction. Mechanics of these movements are hidden in the specialized organ - the pulvinus. We have found that the movements of the petiole, or pinnules, connected to pulvinus are accompanied by a change of the pulvinus morphing structures. This structure has rather peculiar properties similar to the electrical synapse in the animal nerves. Therefore, it was

interesting to investigate electrical circuitry of this organ. Figure 5 shows dependencies of electrical current induced by bipolar sinusoidal wave with amplitude of ±3.5V (a) or ±4.5V (b) and frequency of 0.001 Hz, where platinum electrodes are inserted along the pulvinus of *Mimosa pudica*. There is a pinched point in the hysteresis loop at low frequency of sinusoidal wave in the voltage-current plane when $I = 0$ μA and $V_P = 0$ V, which is a typical sign of a memristor. Figure 5a shows that there is a self-crossing between curves when amplitude of the applied sinusoidal voltage is between ±3.5V. The plot displays a common pinched point without self-crossing between curves when stimulating voltage increases (Fig. 5b). Increasing of a sinusoidal wave frequency to 1 kHz changes the shape of a hysteresis loop and a pinched point disappears. Similar dependencies of electrical current on voltage and exist in a stem of *Mimosa pudica.* There is a pinched point but without self-crossing between curves when $I = 0$ μA and $V_P = 0$ V.

The *Aloe vera* (L.) is a member of the Asphodelaceae (Liliaceae) family with crassulacean acid metabolism (CAM). Figure 6 shows cyclic voltammetry in the leaf of *Aloe vera*. At low frequency of scanning there is a pinched point with self-crossing between curves when $I = 0$ μA and $V_P = 0$ V, which is a typical fingerprint of a memristor. There is also an additional pinched point at the potential of 2 V. Increasing of the speed of scanning from 2 mV/s ($2 \times 10^{-4}$ Hz) to 500 mV/s (0.05 Hz) leads to the disappearance of pinched points in the hysteresis loop. The simple possible equivalent electrical circuits are shown in inserts.

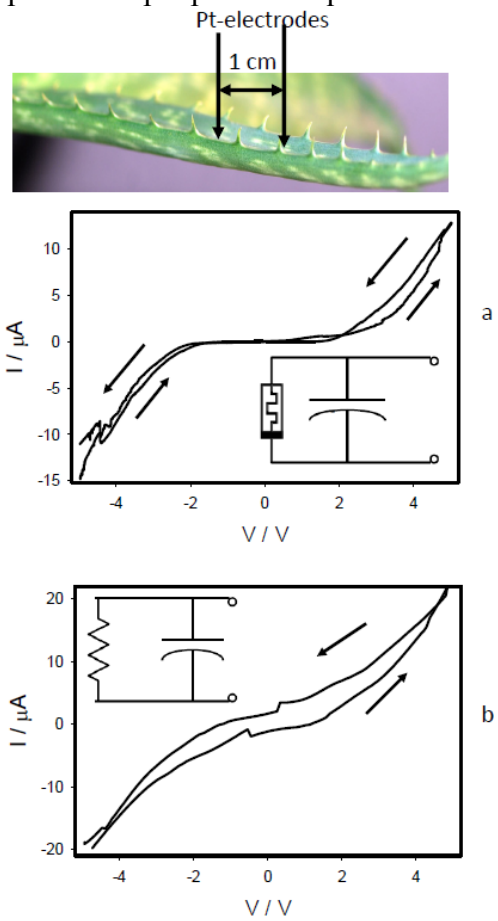


Figure 6. Cyclic voltammetry in a leaf of *Aloe vera* with a scanning rate of periodic triangle wave of 2 mV/s (a) and 500 mV/s (b). Position of Pt electrodes in the *Aloe vera* is shown. The simplest equivalent electrical circuits are shown in inserts. Electrodes were located along the leaf on the distance of 1 cm.

We selected for this analysis the Venus flytrap and the *Mimosa pudica* as dicots, and the *Aloe vera* as a monocot and CAM plant. In all of these plants we found fingerprints of memristors.

It is truly fascinating that even plants exhibit memristor fingerprints. When driven by a bipolar periodic sinusoidal or triangle signal, plants exhibit a pinched hysteresis loop in the voltage-current plane (Figs. 4-6). Starting from some critical frequency, the hysteresis loop changes shape and a pinched hysteresis loop transforms to a non-pinched hysteresis as the excitation frequency increases. Voltage gated channels can exhibit more than one self-intersection points.

The physiology of plants must include memristors as essential model building blocks in electrical networks in plants. The memristor is an "ideal" circuit element and no real-world biodevices can be exactly mimicked by an ideal circuit model. There are different models of increasing accuracy that can be developed at the cost of increasing complexity. Our results demonstrate that a voltage gated $K^+$ channel in the excitable tissue of plants has properties of a memristor. This study can be a starting point for understanding mechanisms of morphing, memory, learning, circadian rhythms, and biological clocks.

Our results demonstrate the role and kinetics of electrical, biochemical, and mechanical events leading to the fast trap closure induced by mechanical or electrical stimuli. There are many quick mechanical movements in plants, and our new hydroelastic curvature theory can be used for understanding and estimating their exact biomechanical mechanisms. The new non-invasive charge capacitor method permits the study of different steps in signal transmission and mechanical responses in the plant kingdom. The study of such a fast and significant response may open the way to engineering applications in many fields, far different to intrinsic plant behavior. Further knowledge of cell membrane physiology, specifically related to the almost instantaneous water and ionic flux after the signal is perceived, could lead to the development of artificial materials with similar properties, with unsuspected applications in science and technology. Our project exploits a new approach to the problem of plant morphing structures. Many plants have the ability to morph and become a shape-changer with optimal performance with low turning radius, long endurance, and high speed. A comprehensive integral project includes development of a new low current measurement system, conduction of very delicate experimental studies, and development of new mathematical model of active movement in plants. This work leads to a better understanding of the mechanisms involved in mechanosensing, high speed movements, electrically controlled morphing, and it will provide the foundation for the development of advanced sensors, highly efficient noise free motors and morphing structures for future DoD and Air Forces applications.

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**Presentations.**

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2. L. O'Neal*, L. Ebere*, R. McIntyre*, M. I. Volkova, V. S. Markin, A. G. Volkov. Electrotonic potentials in plants. ACS Meeting, Abstract Bio.# 310, San Diego, March 25-29, 2012.
3. J. Wooten*, A. Waite*, V. S. Markin, A. G. Volkov. Biological clocks in plants. ACS Meeting, Abstract #365, San Diego, March 25-29, 2012.
4. V. A. Murphy*, A. G. Volkov, V. S. Markin. Venus flytrap: Energetics of plant movements. ACS Meeting, Abstract #367, San Diego, March 25-29, 2012.
5. H. Paulicin*, A. G. Volkov, S. Harris*. Bioelectrochemistry of the Venus flytrap. ACS Meeting, Abstract #366, San Diego, March 25-29, 2012.
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7. A. J. Waite*, J. D. Wooten*, A. G. Volkov, V. S. Markin, Time sensors: Circadian rhythms in biologically closed electrochemical circuits of plants. Abstract #3832, ECS meeting, Honolulu, Prime, October 2012.
8. A. G. Volkov, M. I. Volkova, V. S. Markin, Phytosensors and phytoactuators, Abstract #3827, ECS meeting, Honolulu, Prime, October 2012.
9. L. O'Neal*, M. I. Volkova, V. S. Markin, A. G. Volkov, Propagation and collision of nonlinear electrical responses in *Aloe vera* L. and *Arabidopsis thaliana*. Abstract #1984, ECS meeting, Honolulu, Prime, October 2012.
10. C. Mitchell*, N. Williams*, A. G. Volkov, Charge induced closing of Dionaea muscipula Ellis trap. Abstract #11, ECS meeting, Honolulu, Prime, October 2012.
11. V. Forde-Tuckett*, A. G. Volkov, V. S. Markin, Electrochemical interfaces in plants, Abstract #2830, 224 ECS Meeting, October 2013, San Francisco.
12. A. G. Volkov, C. R. Brown, Citrus greening (huanglongbing): Fast electrochemical detection and phytomonitoring of tree diseases. Abstract #2833, 224 ECS Meeting, October 2013, San Francisco.
13. V. Forde-Tuckett*, A. G. Volkov, Electrochemical interfaces in plants, Abstract #203, 247th ACS Meeting, March 2014, Dallas.